

BRIEF COMMUNICATION

"ROLLERS" AND "CARRIERS": FIELD OBSERVATIONS OF CARRION REMOVAL BY TROGID BEETLES (*OMORGUS STRZELECKENSIS*) IN ARID NORTH-EASTERN SOUTH AUSTRALIA

Despite substantial advances in the taxonomy of Australian beetles (Coleoptera)¹, little is known about the biology and ecology of most of our species, especially those considered of little economic significance. Matthews² suggested that naturalists can make valuable contributions by investigating and describing aspects of the natural history of beetles. Often such observations are opportunistic and represent situations difficult to replicate in the laboratory. With a minimum of equipment, many useful aspects of behaviour can be noted and simple experiments used to clarify observations.

During a recent limnological field trip to the Coongie Lakes area, an opportunity arose to study groups of carrion beetles (Trogidae) transporting faecal pellets and regurgitated egesta along a sand-dune on the western shore of Lake Goolangirrie (26°53'S 140°06'E), 112 km NW of Innamincka, in the Innamincka Regional Reserve. The lake fills as a result of overbank flows in the North-West Branch of Cooper Creek. This lake, and many others nearby, owe their irregular shapes to the extensive dune systems running approximately north-south, and vegetated by an open tall shrubland of *Acacia ligulata* A. Cunn. ex Benth. in the wider swales, a hummock grassland dominated by *Triodia baredowii* E. Pritzl along the major dune systems and sand-hill cane-grass (*Zygochloa parviflora* [R. Br.] on the mobile dune crests³.

The beetles were identified as *Omorgus strzeleckensis* [Blackburn, 1895⁴] described from specimens collected near Lake Callabonna and Strzelecki Creek. The species is widespread throughout mainland Australia, occurring in low rainfall areas of all States except Victoria⁵. It is distinguished from congeners by the combination of shape of the elytral costa and the single large median tooth on the fore tibia. Scholtz⁶ noted that specimens had never been collected in January, April, June or December — my observations were made in December (early summer).

Life history data on the Australasian Trogidae are few although some 53 species have been described, of which two are introduced⁷. The only published record of a particular feeding habit appears to be that by Leefmans⁸ who reported *O. (Trox) costatus* living and feeding on bat guano in caves in the Celebes (Sulawesi). In Africa and America, trogid adults and larvae are facultative necrophages and generally appear late in the succession of invasions of carcasses in the arid zones of these continents.

Three broad strategies for coprophagy and necrophagy in arid zones are recognised⁹. The first is to tap the latent moisture of the particle and to breed as quickly as possible before it dries (e.g. dipteran flies, especially calliphorids). Alternatively, the material may be comminuted and buried to conserve its moisture as is the case with dung-beetles (Scarabaeinae). In arid areas, the lack of reliable rain leaves some species of dung-beetles underfed because they can bury desiccated faecal pellets that rehydrate from soil moisture⁷. Finally, some groups (hermites, tenebrionids, trogids) are able to eat dry faeces and mummified carrion. *Omorgus (Trox)* spp. can complete their life cycle on only wool clippings or even discarded wool clothing⁷.

Omorgus spp. in the Kalahari Desert are morphologically, behaviourally and physiologically adapted to survive long periods of aridity interspersed with brief favourable periods when feeding and copulation occur⁹. Adults and larvae quiesce under adverse ambient conditions, renewing activity within hours of amelioration. Immature stages develop rapidly (3-4 weeks³) whereas the adult lifespan is long enough to allow overlapping generations. The availability of mummified carcasses of large antelope for several years allows populations to build up below the remains without the risks involved in dispersal to seek food or mates⁹.

The following observations were made over two days (10-11.xii.1991). Tracks consisting of numerous small depressions in a band 3-4 cm wide were noticed running east-west along a dune face soon after sunrise (0630 hours) on 10.xii.91. They were made by two beetles carrying a tapered dingo faecal pellet measuring approximately 3 cm long and 1 cm in diameter (Table 1). The beetles were moving westward, and a light easterly breeze was blowing when detailed observations commenced at 0645 hr. Subsequently, six other groups of beetles were discovered carrying or rolling egesta from the base of a lone Coolibah tree (*Eucalyptus microtheca* F. von Mueller) growing halfway up the dune face. These groups, noted at about 0700 hr, when the breeze had strengthened slightly and swung to a northerly, were moving southwards and had travelled only several metres.

The most striking feature was the two different modes of carrion transport adopted by the groups of beetles. They either carried or rolled the egesta, depending upon its shape. Irregular pieces of carrion were physically carried upon the backs of the beetles with the load being spread fairly evenly between individuals. The pieces of carrion were stabilized by nodules and grooves on the pronota and elytra of the beetles. More cylindrical pieces were rolled along. Beetles propped their stout forelegs against the carrion or hooked their pronotum under the edge of the particle, lifting their heads while pushing forwards with their middle and hind pairs of legs. Although the beetles were always on the trailing edge of the rolling piece of carrion, they often appeared to push each other forwards and it was not unusual for a beetle to walk over the backs of others to roll the particle.

It is important to distinguish between these two types of carrion transport by trogid beetles and the classification of resource relocation that is frequently applied to the majority of dung beetles. Dung beetles are separated into guilds of tunnellers (paracoprids), dwellers (endocoprids) and rollers (telocoprids)^{10,11}. Tunnellers dig burrows immediately below the dung and push pieces of it into the tunnels, dwellers live and feed within the dung heap itself, and rollers make balls of dung that they roll away from the food source and other beetles before concealing them in the soil¹². In the case of the trogids that I observed, all the beetles would be in the roller guild¹¹ but exhibit either carrying or rolling behaviour. In dung beetles, the guilds are species specific whereas the modes of particle transport evident in the trogids in my study both occur in the one species.

TABLE 1. Summary of observations made on seven groups of carrion beetles at Lake Goolangirrie. Means (\pm SEs) are for all groups carrying egesta southwards (group 1 is excluded because it was carrying a faecal peller west).

Group	No. of beetles	Size of burden (cm)	Shape	Transport mode	Track length (m)	Mean gradient (%)
1	2	5 \times 1	Tapered	Carrier	31	20
2	5	6 \times 7	Irregular	Carrier	35	10
3	5	6 \times 3	Cylindrical	Roller	28	17
4	3	8 \times 2	Irregular	Carrier	28	18
5	3	5 \times 2	Irregular	Carrier	40	11
6	3	2 \times 2	Cylindrical	Roller	42	7
7	5	9 \times 2	Irregular	Carrier	45	7
Mean	4	6 \times 3			36.33	11.67
SE	0.45	1.00 \times 0.82			2.95	1.96

The inclines up which the carrion was rolled or carried were measured by holding a metre stick horizontally level with one end resting on the track and the stick pointing along the path taken by the beetles. The elevation of the free end of the stick measured the rise (in cm) over 1 m and was expressed as a percentage (Table 1). The maximum incline up which beetles rolled carrion was 30% whereas particles were carried up a slope of 42%. The shape of the carrion particle appeared to determine its mode of transport rather than the slope of the incline or the number of beetles involved (Table 1). In general, there were more beetles associated with larger pieces of carrion but other factors such as particle shape are probably also important. By placing small flags along the tracks at 30 or 60 second intervals and measuring the length of the path, I was able to compare the speeds of carrion transport by the two different modes. At temperatures of 26–28°C and traversing similar terrain, five beetles carrying egesta (Group 2, Table 1) moved faster than a group (3) rolling a smaller piece (Table 1). "Carriers" averaged 0.42 cm.s⁻¹ ($n = 10$ determinations, SE = 0.03) whereas "rollers" moved at 0.28 cm.s⁻¹ ($n = 9$, SE = 0.02).

The pathways were not straight but meandered in a general direction. When the egestum became wedged against a stick or embedded in a hollow, the beetles soon retraced their steps and circling around, tried a slightly new bearing. These circles never exceeded 30 cm in diameter and I only found one piece of carrion that became inextricably trapped in a clump of *Enehaena tomentosa* R. Br. (Group 5). The following day, this particle was covered in ants and there was no sign of the carrion beetles nearby or buried below.

At times, individual beetles would wander away from the carrion or become dislodged after a particularly vigorous roll. Invariably, they would circle to the downslope side of the carrion and then travel with the wind, moving uphill until they were directly downwind of the particle. Immediately, the beetle would turn towards the carrion and walk in a straight line up to it, even if the particle was out of the direct line of sight due to hollows and sand ripples. I observed this behaviour several times, and successful reunions occurred over distances of 2 m. When a member of the group wandered away or was dislodged, the rest of the group did not alter behaviour and continued moving the egesta.

Beetles were able to sense carrion from a radius of 10–15 cm even if upwind (as "rollers" often were) and moved directly towards the particle. This was confirmed experimentally using

both "rollers" and "carriers", and was possibly visual. Shubock¹¹ observed that carrion beetles in the family Silphidae could detect odours at distances of approximately 1 m when air movement was negligible but at greater distances (5–75 m), he concluded that orientation to carrion was due to random wandering.

If beetles go to such lengths to transport carrion, do groups exhibit any possessiveness, perhaps defending their particles from other conspecifics? Anecdotal evidence from field observations indicates that inter- and intra-specific competition among dung-beetles can be intense, ranging from direct combat when beetles fight over the possession of dung to scramble competition when the beetles' activity at high densities prevents most individuals acquiring sufficient resources for breeding¹⁴.

What happens if a wandering beetle trying to recover its carrion finds itself downwind of another group's particle and homes in on that. Can a wandering "roller" readily switch to "carrying" if an irregular piece of carrion is encountered? To examine these possibilities, I planned a series of transfers of beetles from one group to another, within and across modes of transport. Touching the beetles caused them to feign death instantly, becoming immobile and tucking their limbs tightly under their body. Thus, it was necessary to allow them to walk onto a strategically placed leaf and then transfer the beetle quickly, placing it just downwind of the carrion in all trials.

In all transfers ($n = 5$), there was no change in the behaviour of the recipient group and I was unable to detect any physical antagonism. Newcomers often crawled over the carrion for several seconds before joining their fellows either rolling or carrying the particle. I returned all beetles to their original positions at the end of the experiment, where they resumed their behaviour, seemingly unaffected by their brief transfer. Thus, it seems that groups of beetles of this species are not especially protective of their carrion resources. It would be interesting to add beetles continually to a particle to see if intraspecific competition could be induced. Beetles had no apparent difficulty switching modes of transport to match that of their fellows — in no case, did they try to roll a particle that was being carried or *vice versa*. Furthermore, I never observed a group of beetles switch modes of transport in response to a change in grade or substratum particle size.

I also found an eighth group of two beetles rolling a cylindrical piece of egesta (2 \times 3 cm) southwards. I sacrificed these two beetles for identification, and with three others,

they are lodged in the South Australian Museum (classified with the Trogidae, Dr Eric Matthews, South Australian Museum, pers. comm.).

Could beetles be enjoined away from their carrion by another, seemingly palatable piece of egestum, especially given their apparent lack of possessiveness? When this was done, groups of beetles carried or rolled their particles past the new piece, even when it was placed in the path of the group. However, if a single beetle became separated from the group and the particle was placed in its path, the beetle crawled over the carrion in a similar exploratory fashion to that observed earlier and then proceeded to either roll it or to burrow below it.

The morning I made these observations was overcast but sand temperatures rose gradually from 18°C at 0700 hr to 34°C by 1000 hr. By 0900 hr (26°C), Group 1 carrying the dingo faecal pellet to the top of the dune had burrowed below the pellet leaving it exposed. However, sand blown by the wind had half-buried the pellet and completely obliterated the tracks by 1100 hr. At 1115 hr, sand temperature reached 40°C and the other six groups of beetles ceased activity almost instantaneously. The wind had strengthened and air temperature was 35°C. In all cases, beetles either sheltered below the carrion or had burrowed into the sand beneath the particle to a depth of 3–5 cm ($n = 3$). Observations of depth of burrowing were restricted to groups 2 and 3 ('carriers' and 'rollers' respectively). For the rest of the day, the beetles remained inactive.

At 1910 hr, activity around several particles (2, 3, 4, 5 and 7) resumed. Air temperature was 28°C, sand temperature was 27°C, and the wind had dropped. However, humidity was extremely high and intense electrical activity overhead heralded a thunderstorm which broke at about 2000 hr. Up to this time, beetles in groups 2 and 3 had moved their carrion several metres south, and group 4 had carried their particle 12.3 m north. The beetles in group 7 had moved around in a circle (10 cm diameter) surrounding their carrion and then apparently burrowed, leaving pock-marks several mm broad in the ground. Activity ceased completely during the rain from the thunderstorm which effectively ended my observations.

There were no tracks or activity the following morning, which was sunny and 18°C at 0600 hr with a gentle southerly. The rain had soaked to 1.5 cm and although I was able to recover several half-buried, bedraggled pieces of egesta, I was unable to find any beetles even though I destructively excavated each spot where the observations had ceased during the storm. It was not clear whether the egesta had been buried by the beetles or, more likely, wind-blown sand and rain.

Presumably, the beetles had either dispersed individually or had carried and buried the carrion in the intervening 10 hours.

Why do these beetles go to such lengths to transport the egesta? One adaptive explanation for this form of behaviour in dung beetles is that the action reduces competition for the resource from rivals of the same species or other species that consume dung¹⁵. Alcock suggests that had the beetles remained at the site of deposit, the concentration of material might have had a higher probability of attracting vertebrate scavengers or ants that could consume the egesta before the trogids. Possibly, the beetles themselves would then be put at risk as a nearby food resource.

Another explanation has been applied to dung beetles in the tunneller and roller guilds that need to transport the particle from an area where it may have fallen on ground that is unsuitable for burrowing or that is too exposed to harsh ambient conditions¹⁶. This does not mutually exclude the first hypothesis and may also be a valid explanation for the trogid behaviour observed in the present study. On an unstable sand dune, buried egesta are likely to be exposed by wind whereas in areas stabilised by vegetation, this risk is lessened. Further, local soil moisture is likely to be greater, perhaps enhancing the food quality of the carrion. Relative humidity is an important factor controlling the behaviour of two species of Kalahari *Omorogus*¹⁷. High relative humidity restricts respiratory water loss, improves food (moist hair and keratin) quality and may compensate for faecal water loss¹⁸. Perhaps the trogids I observed were transporting their particles long distances until they found clumps of shrubby vegetation where relative humidity and sand stability were high and food quality would be enhanced when the particle was buried. This hypothesis awaits testing.

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